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ANIMAL IMPROVEMENT AND ADAPTATION

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ANIMAL IMPROVEMENT AND ADPTATION

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What is Ideal?

1. The first step in an animal improvement program is to define what kind of animal is "best" for the purposes of the people in the country concerned. That means considering not only the human needs for the products of these animals, but also the qualities of the animal itself which will promote its own well-being. Even religious or other cultural values may bear importantly on whether surplus animals or those of little merit can be killed and whether animals have values as symbols of their owner's social status or wealth. Usually only a local person or at least one who has lived in the country for several decades can know the culture of the people well enough to realize the true value of livestock in that society, but this may seriously modify the objectives of an improvement program. Human needs concern such things as milk, meat and eggs for human food; work; wool, hides; etc. The animal's well-being can depend to some extent on such things as its tolerance to heat, cold or rain; its ability to withstand inadequate nutrition during certain seasons; its resistance to diseases and to insect pests; etc.

Individual Merit

2. Measurement or appraisal of an animal's merit merely expresses how closely that animal conforms to the ideal. Merit may be defined either phenotypically or genetically. The former involves only the animal's own observed qualities. The latter concerns the kinds of offspring and other descendants the animal is likely to have. An animal's genetic merit can be estimated only indirectly by considering its own phenotypic merit and also the phenotypic merits of its available relatives. In considering all of these phenotypes the effects of variations in the environment should be discounted as much as possible.

3. The simplest definition of individual merit may be merely a verbal description. A score card is a somewhat more quantified description. A selection index is a score card modified still further by such knowledge as we have of heritability and genetic and phenotypic correlations among the constituent qualities. The selection index is intended to rank the animals according to their value for breeding purposes (i.e. according to their genetic merit); whereas the ordinary score card ranks them only phenotypically according to their own appeaance or performance.

4. The individual merit that concerns the modern breeder is in productivity, rather than in bodily form. The measurements of productivity should be as direct as possible, such as: Weights of fleece or of milk produced; weights of young reared to weaning; growth rates in general; longevity; life-time production; etc. Although such measures do not show an animal's real and complete productivity with perfect accuracy, they are so much more accurate than easily observable external "sign characters", such as color, shape or size of horns, shape of head, size of skeletal frame, conformation of legs, etc., that the latter have only faint utility. The wide popularity of "sign characters" is due mostly to human nature and to the ease of observing such "signs".

5. Practical merit involves many characters, several of them important, but the whole animal is the smallest unit which can be selected or rejected. Therefore, one simply must add (or combine in some other way) an animal's high merit in one quality, medium merit in another, and low merit or defectiveness in others, to decide whether to keep or cull the animal. This combination we call "net merit", realizing, of course, that in some cases net merit can be for breeding. The measurement of merit must be kept simple for practical reasons but it is complicated by the fact that many qualities enter into it, some of which are of minor importance. The following procedure seems to work best: Measure as directly and simply as possible the 2, 3 or 5 most important aspects of productivity and allot to them about 60 to 80 points. Then group together all the remaining characters which contribute enough to merit to be worth considering, calling this group by some such term as "general appearance" or "other qualities". Allot to this group the remaining 40 to 20 points on the score card. More detail and refinement of records and their use will be worth while, only if it increases the accuracy of choices enough to be worth more than the costs of the extra work. However, this is not likely to be feasible in the first programs in the less developed countries, but that is a matter for local decisions and ingenuity.

6. What one will actually do at a given moment, on the basis of these ratings of merit, is simple. Either he culls the animal or keeps it for breeding purposes. If he keeps it, he may also need to decide whether he will keep its sons as well as its daughters, or will keep only its daughters. For the animals which are retained now, decisions may need to be made again next year when new information has become available.

Improvement by Breeding

7. The basic principle is that the animals which are closest to the ideal in their genetic merit should be used most extensively for breeding, while those furthest from the ideal should be culled at the earliest opportunity. Performance testing is done to measure phenotypic merit. Progeny testing, as well as information on parents and collateral relatives, come into the picture only as they help to correct some of the mistakes which would be made if decisions about each animal were made entirely on its own phenotypic merit. Artificial insemination comes into the picture only as it permits more intense selection among the males thought to be best. It does not change at all the kinds of genes the chosen sires transmit. Also it can make importation less expensive by getting more offspring per imported sire. With artificial insemination, therefore, the importance of deciding correctly which males are really best for breeding use is increased, since fewer males are used and any mistakes made in choosing one of them will affect more individuals in the next generation.

8. Improvement in animal breeding can follow two different roads. These have some things in common but are mutually exclusive in others.

9. The first road, the traditional one, is to select the best and cull the worst in the hope of improving the whole stock more or less steadily. The ultimate goal is to produce a stock which is fully as perfect as any cross which could be made from it. In genetic terms, this is hoping to make a stock homozygous for all the "good" genes and free from all hereditary defects. To this end, attention to ancestors, collateral relatives and progeny, are mere devices for making selection more accurate and therefore hastening progress. In traveling this road, line-breeding is used as a holding action, whenever an unusually good animal appears, and also to harvest some of the epistatic effects by bring together repeatedly in favorable combinations genes, which in other combinations are unfavorable. Otherwise all forms of inbreeding are avoided. If this road really is traversible, it is the simpler of the two.

10. The second road leads toward a situation in which seedstocks are bred separately from each other but are outcrossed, in one way or another, to produce animals for use. This can be called breeding for heterosis. This road may be the best one when, in many pairs of genes, the heterozygote is individually preferable to both homozygotes. This may happen for a variety of genetic reasons, which will be mentioned briefly later. Since the seedstock animals are to be crossed on those from a different seedstock, the practical test of the individual breeding merit is the average merit of the crossbred progeny they produce with that other stock. This road relies more on the progeny test and much less on individual merit of the animals in the seedstock than does the other road. The important thing is that the progeny by which an animal's breeding value is judged shall be out of crosses with the same kind of stock as that on which it is expected to be used when producing animals for use. The pure seedstock is to be improved not in its own individual merit, but in its ability to produce good crosses.

11. This second road, if ultimately successful, would lead to pure seedstocks which are only mediocre or less in individual merit but cross with each other to produce individuals which average better than any purebred population which could possibly be produced by travelling the other road. This second road is currently being used in the United States in producing hybrid maize and in practically all of the poultry breeding. The methods of forming the various seedstocks may be simple intense inbreeding, which is the usual one in maize, or more complicated systems, such as "reciprocal recurrent selection", may be used.

12. Crossbreeding is a way to travel this second road, a method already widely practiced with some farm animals in some parts of the world. Instead of starting by making new seedstocks especially well adapted to crossing with each other, one merely finds which of the already existing breeds, or other genetically separate stocks, cross well with each other and then proceeds to use those at once. Formerly it was usually recommended that all of the crossbreds, both males and females, be sold and none of them be saved for breeding. The generally succesful work on "crisscrossing" at the Minnesota Station and elsewhere which began to be published in the 1930's cast doubt on this recommendation. The experiments with 3-breed and 4-breed rotation crossbreeding, which began late in the 1920's have tended to confirm the conclusion that the replacement females can come profitably from the crossbred stock. This also agrees with the extensive experiments of the maize breeders and, as far as they go, with the experiences of the poultry breeders.

13. All that remains important is that the males shall be purebreds from breeds which cross well with the breeds from which the sire (and preferably also the maternal grandsire) of the females come. Even crossbred sires may be used, provided both are breeds which were crossed to produce the sires and maternal grandsires of the females on which these crossbred sires are to be used. Naturally, this last condition is rarely met. The use of an actually crossbred sire is still generally regarded with disfavor by animal breeders, although it is standard practice in the breeding of maize and of some chickens, particularly among the egg-producing crosses.

14. Such crisscrossing or rotation crossbreeding could begin at once in the less well-developed countries if one or more breeds can be found and imported which cross well with each other and with the native stock. The native stock are likely to furnish some useful local adaptability. In a crisscrossing system in which the natives constitute one of the stocks, the percentage of native blood will vary from 33 to 67 after the system gets well under way. In a regular 3-breed rotation, it would vary from 1/7 to 4/7. The producer need not buy females. It is important, however, that someone in the country continue to breed enough pure native stock to furnish the native sires needed at one step in the rotation.

15. Trying to travel this second road without using the existing stocks or breeds at the very beginning would be unwise for any of the less well developed countries. Making new and relatively pure lines would be expensive and would require several generations, whether they were made by inbreeding or by selecting on progeny tests for cross-combining ability. Much expensive and detailed progeny testing and other record keeping would be necessary. This may not be feasible in such lands, and waiting so many years to harvest the increased productivity may be impossible. Even in the countries where animal breeding is highly developed, it is not certain that making seedstocks expressly for their increased cross-combining ability will ever be feasible for types of animals that are less prolific and which have longer generation intervals than swine. Even with swine the practicality of this road is still in doubt.

16. Crosses often have higher average individual merit than either parent race. This is generally called "heterosis". It is rather frequent but it does not occur for all characters nor in all crosses. To gain the benefits of heterosis is the chief reason for using breeding plans which are more complicated than simply finding and breeding the best individuals, while culling the worst as opportunity offers. To see how the gain from breeding for heterosis might be large, consider a case of simple over-dominance where AA averages 100 on the scale of merit; Aa averages 110; and aa averages 70. If these contribute offspring to the next generation in proportion to their own merit, the population will reach a ceiling where it consists of .64 AA: 32 Aa: .04 aa and its average merit is 102. Selection cannot increase its average merit further, so long as the individuals interbreed freely. To select more intensely for the Aa's would lower average merit by making the aa's more frequent, while selecting more intensely for the AA's would lower merit by making the Aa's rarer. The constant presence of 4 percent of definitely inferior aa individuals in the population is the price paid for raising the average merit of the population to 102, instead of leaving it at 100 where it would be if the population were homozygous for the "best" gene; i.e. were pure AA. If, on the other hand, one could make and keep two separate pure seedstocks, one aa and the other AA, and could cross these to produce the animals for use, this crossbred population would average 110 in merit. The cost of securing this gain from 102 to 110 would be the costs of making and maintaing the two pure seedstocks which, in their own merit, would average only 700 and 100, respectively.

17. Heterosis in net merit can occur even where the cross does not exceed the better of the two parent races in any character. All that is necessary is for the one parent race to be superior in some respects and the other in other respects, while the cross tends to be nearer the better parent in each case. This is illustrated schematically by the following figures where equal weight is given each character.

	Race		
	A	Cross	B
Merit in character No. 1	100	98	80
" " " " 2	90	96	100
Average Merit	95	97	90

18. This is a rather common situation in crossbreeding. Usually a breed will be chosen for a cross only if it has some characteristics in which it excels and, since it is not perfect, it will fall behind the other breed in some other qualities. If several characters are involved and if the cross is nearer to the better parent in each, the cross is likely to excel both parents in net merit, even though it may not excel the better parent in any one character considered singly.

19. Several genetically different mechanisms or situations can cause heterosis. They include such diverse things as:

a. Each parent race having some of the desired characters which the other lacks (discussed above).

b. Simple overdominance in one or more pairs of genes (the order of merit is Aa-AA-aa).

c. Year-to-year or place-to-place variations in the environment, whereby sometimes one and sometimes the other parent has the higher merit. This is partly the same as (a).

d. The heterozygote is better buffered against the environmental changes than the homozygotes are. This is partly the same as (c).

e. The population is not entirely at linkage equilibrium.

f. Pleiotropy whereby each gene has several effects, some good and some bad. This may be the main cause of (b).

g. Some of the desired characters may be partially antagonistic to each other genetically. This partly overlaps (a) and (f).

h. Epistatic effects in general. (The simplest case is where two non-allelic genes together produce desirable effects although their average separate efforts are undesirable.)

All of these causes of heterosis require some dominance. Most of the immediate and observable consequences are the same as if the heterosis were all caused by (b), although the results can become different in later generations, especially if (a), (e), or (h), cause much of the heterosis.

20. The amount of heterosis expected in the first cross between two stocks which have each been breeding within themselves depends mainly on the degree of dominance and the genetic diversity of the two stocks. Each pair of genes contributes to the heterosis $(k-1)\ (q_1 - q_2)^2x$; where k is the degree of dominance on a scale from 1 for no dominance, through 2 for complete dominance, to more than 2 for overdominance; q_1 and q_2 are the respective frequencies of that gene in the parent stocks; and $2x$ is the average difference between the phenotypes of aa and AA. Half of this is permanent; the rest disappears at once and entirely from the offspring when first crosses are mated together, -- somewhat more than half of it disappears if 19 (h) is a major cause of heterosis. A little of the half of heterosis which is temporary can be retained by continuing to outbreed, as by backcrossing, crisscrossing, mating those from the most unrelated families, etc. The $(q_1 - q_2)^2$ term, which measures the genetic diversity, indicates roughly how much can be retained thus.

21. In a system of rotation crossbreeding where the females are always mated to males with a percentage of blood as different from theirs as is available, the percentage of heterozygotes remains higher than it would in a pure breed made from any of those crosses. This is the basic genetic reason for using a rotation crossbreeding system wherever the heterosis is large and the economics of the case and the kinds of animals available will permit.

22. The following actual data from the Inter-American Agricultural Institute in Costa Rica illustrate marked heterosis in daily gains and practically no heterosis in muscle area.

Breed or Cross	Daily gain (grams) (corrected for sex)	Muscle area ($cm.^2$) (males only)
Brahman (Zebu)	602	64
Criollo	495	80
Criollo X Brahman	622	78
Brahman X Criollo	691	70

In daily gain the two crosses exceed the average of their parental races by 73 and 142 grams, respectively. In muscle area the two crosses differ little, either from each other or from the average of the parental races.

Deception by Heterosis

23. When the first cross offspring of imported males and x native females seem definitely superior to the native stock, it would be only human to credit all of this improvement to the imported sires, especially if purebreds of the imported race are not available for comparison. This, however, may not be valid. The crosses may also be superior to what the pure imported stock would be if grown under the same conditions.

24. In the example of cattle gains in Costa Rica, if we had data only on the Criollos and on the cross of Brahman bull and Criollo cow, we might infer that the Brahmans were vastly better genetically than the Criollos. If, however, data were available only on the pure Brahmans and on the cross of Criollo bull and Brahman cow, it would have been inferred that the Criollo was better than the Brahman. With data from all four of these combinations we conclude correctly that the Brahmans do gain somewhat more rapidly than the Criollos, but that the crossbreeding effect itself is tremendously larger than this difference. This is a measure of what is called "heterosis". By contrast, in muscle area, the Criollos have definitely larger muscles than the Brahmans and the heterosis seems small.

25. If we know only one pure breed and one pure cross, we can be vastly misled in inferring the merit of the other pure breed. For example, if we know the rate of gain only for the Criollos and for the cross of Brahman bull on Criollo cows, we might infer that the favorable results were due to the general merit of the Brahman breed. Then we might think that the rate of gain of the pure Brahman would be 887 (i.e. 691 + (691 - 495), plus or minus whatever allowance we thought proper for the data being few! We would estimate that if we made a second cross to the Brahman the 3/4 Brahmans would average 797 (i.e. (691 - 495)/2) whereas, if we know the data for all 4 kinds of breeding and allow for loss of heterosis, we will expect only 629 (i.e. half of (691 + 622)/2 + 602) for the 3/4 Brahmans.

26. As another example in which, however, only one of the reciprocal crosses is present, consider the following data from the same station for average 4% fat-corrected milk production of stablemates in kilograms during each of the first four months of the first lactations.

	Month			
Breed or Cross	1st	2d	3d	4th
Criollo	266	230	224	189
Jersey	237	226	202	178
Criollo X Jersey	273	248	245	254

Heterosis is nearly 9 percent in the first two months, 15 percent in the third and 38 percent in the fourth. This is the evidence on the amount of heterosis in this character in this cross, although one may wonder whether reciprocal crosses would show any differences, such as might be caused by sex-linkage or by maternal effects.

27. Heterosis should be estimated early in the process of planning to improve the native stock by using sires imported from some supposedly superior breed. The amount of heterosis might alter decisions on such important matters as whether: 1) to continue grading the native stock to an imported breed, 2) follow a plan of rotation crossing, or 3) try to make a new breed, moderately stabilized at some fraction of imported and native blood. The larger the heterosis, the more important a practical plan for 2) becomes.

Importing

28. As soon as one has decided what kind of stock would really be ideal for his purposes, he seeks the breeding stock which is already nearest that ideal. The native stock should be considered first, as it is the most available, almost always the cheapest, and usually already has considerably more adaptability to local conditions than any stock which could be imported. Although well adapted to survival under the local conditions, they are likely to be slow maturing, thinly muscled, and not likely to produce large quantities of milk or wool, or other of the products which a developing country needs. However, before deciding that the native stock is not suitable, it may pay well to visit all of the possible places where such native stock has been improved by the better local breeders. Some of these local efforts may show definitely that the local stock contains many advantageous qualities which are hidden now but which will come to light when the animals are given better care and are selected for more production. One cannot thus estimate the ultimate to which the stock might be improved, but, if even a few breeders have already made obvious improvement, it is likely that those

limits are still far off. At least, one may infer that the local stock has enough obvious or hidden merit that it should not be replaced entirely but should be retained as one of the stocks to be used in a rotational crossbreeding program or as part of a foundation from which a new breed is to be made.

29. Improvement by breeding is a slow process. Hence, it might be quicker to import an already improved stock if a productive one can be found which is adaptable to the local husbandry. Whether such stock exists is difficult to determine. The excellence of an improved stock in its native land may be due largely to the good nutrition and other excellent environment given it there. One of our colleagues active in extension work in dairy cattle breeding in the U.S. has often said: "No bull was ever good enough to transmit to his daughters good pastures and leafy green alfalfa hay"! How the imported breed will perform in the importing country can be learned only by trying it there. This, however, is costly in time and money. Some of that often can be saved by visiting other countries, somewhat similar in climate and other environmental conditions, to see how any breeds they have imported have actually thrived. Verbal testimony about performance may need discounting, since at least a few enthusiasts about almost any breed can usually be found.

30. An imported breed is rarely suited perfectly to the local needs. Occasionally a breed may fit the local needs well enough that the wisest course is to import that breed and use the males to grade the local stock continuously toward that breed. In such a case, importing also a few females might be wise for two reasons. First would be to learn how well the females of that pure breed perform under local conditions. If the native stock is graded continually toward this imported breed, the resulting high grades will eventually be much like the imported purebred females genetically. If the purebred females are ill-adapted to the environment in any important aspects of their performance, that should be discovered before the grading goes far. Secondly, the sons of the imported females could be used for continuing the grading process. This would reduce the amount of importation necessary for replacing the initial purebred males. Using sons and grandsons from such a nucleus herd need not lead inevitably to high inbreeding. As long as the breed continues to exist in its native land an occasional importation, perhaps at considerable expense, of fresh stock to be used on the nucleus herd would cancel at once the inbreeding accumulated up to that time.

31. The native stock should be very nearly equivalent to the imported stock by the time it has been graded up to contain 7/8 or more of the imported blood, unless improvement in the native land of the breed continues much more rapidly than in the importing land. In such a case, which is rather unlikely but not utterly impossible, continuing indefinitely into the future to import a few animals from the original home of the breed at frequent intervals may be advisable.

32. More frequently, it will be found that no breed exists which is already this well adapted. Each of many breeds which might be imported may be desirable in some characteristics such as ability to produce milk, wool or meat when properly fed; and very undesirable in others, such as adaptability to extreme heat or cold, or susceptibility to parasites or diseases, or to other environmental influences different from those in their native land. Desirable characteristics tend to be partially dominant. Some heterosis often occurs when strains very unlike in their racial origins are crossed. Hence, the first crosses of imported stock on the native stock often appear more desirable than the natives and also more desirable than the pure imported stock would be. Continuing to grade toward the imported stock, generation after generation, will then cause a decline in average merit, partly because the animals are losing the adaptability of the natives and partly because they are losing heterosis.

33. Two quite divergent roads to meet this situation are imaginable. One is to try to make a new breed out of the first crosses, or perhaps out of a mixture of first crosses and back crosses, hoping to form a new breed which will be more than half-way toward the qualities of the better breed in each respect. The other road is to adopt and continue some form of rotation crossing, first, toward the one parent stock and then toward the other. This requires maintaining both of the parent stocks in a usably pure condition. If successful it maintains more heterosis than if all of these animals were mated at random.

Making New Breeds from Crosses

34. When no existing breed comes close to the ideal but each of two or more have some different desirable characters and some of these crosses are known to be promising and heterosis seems not to be large when each character is considered by itself, trying to blend them into a single new breed may sometimes be wise, although this will require so much time that its advisability in a less well developed country may be questioned.

35. The first step is to decide what crosses one should make and in what proportions. Naturally, one would want to use enough breeds to introduce all of the qualities he thinks he will need eventually. Of course, also he would want to use a larger fraction of blood from the races which had several desirable traits and were nearer to his ideal than from races which had only one or two desirable characters which the other races lacked. At least two generations are required to bring together the inheritance from three to four different races. At least three generations are necessary if five or more are to be brought together.

36. The second step is to discount the effects of heterosis. Unless one does this, he will be unduly disappointed in the generation when all the temporary heterosis first disappears. That will be the first generation produced by mating together males and females which have the same percentage composition of blood. Then for the first time one sees the average phenotypic merit of the population with which he is really starting to make a new breed.

37. A third important part of the plan is to keep the genetic base broad. Neglecting this appears to have been the major cause of failure in most of the past attempts to form new breeds which were successful initially. To keep the genetic base broad, present knowledge of genetics suggests that every generation of animals saved for breeding should include the offspring of four or five widely used males. This might mean starting 10 or 12 males in service each generation or it might mean starting as few as 5 or 6, depending on how many of the males that were first tried were later culled on the basis of progeny tests, along with most of their offspring. This should keep the genetic base broad enough that no trouble would arise from this source, at least within the next 6 or 10 generations of animals.

38. Failure to keep the genetic base broad is most likely to arise through not using enough different sires in each generation. For instance, if only one sire is used, or if 4 are used but one of these does so much better that all 4 of the sires saved for the next generation are sons of this one, it will soon happen that any mating which can be made and still remain within the limits of the new breed will involve more inbreeding than is safe. Most of the bad consequences of such inbreeding, especially those from numerous genes with individually small and harmful effects, can then be repaired only by a wide outcross. Such a wide outcross would also undo most of the favorable progress already made.

39. When trying to make a new breed, the pedigrees should be planned roughly for the next two or three generations. That means choosing now the group of females from which are to come the males to be used in the next generation and choosing a somewhat larger group from among whose daughters are to come the sires to be used in the second and third generations. Mendelian segregation introduces enough chance and uncertainty that one is usually wasting time if he plans today the exact pedigree of an individual sire he intends to use 2 generations from now.

40. If the new breed is to be used commercially as nearly pure for its own qualities, rather than to be used in a rotation crossbreeding scheme, the new breed would be made as a single large population with only slight subdivision into families. Such subdivision would be for line breeding or progeny-testing purposes and with the intention of top-crossing the best families on all the rest of the stock as soon as the best ones are identified. If, on the contrary, this new breed is being made for use in a rotation crossbreeding plan, one would want to produce at least one other stock to be rotated with it in that crossbreeding and he would want to keep these two or more stocks genetically as unrelated to each other as possible.

41. Other practical considerations enter the problem, such as the fact that the females of the native race may be better grazers or otherwise better adapted to the local environment, so that the cross made one way may give better results than the reciprocal cross. Factors such as difference in mothering ability and the probability that the imported race and the native race were not equally far from the goal initially, make it sometimes advisable to choose a level of 1/4 imported blood, or of 3/4 imported blood, or some fraction other than 1/2 as the best percentage of blood around which to make a new breed or around which to oscillate in a crisscrossing plan. The question of what is ideal in this respect may well have different answers for differing breeds and different crosses in different countries. Being familiar with the country and with the actual average performance of different mixtures is of the utmost importance for making correct decisions on points like this.

Individual Adaptation

42. An animal taken from its native country to a land with a distinctly different climate may require many months to adjust its own individual physiology in the new environment. If the animal is mature when imported, it may never complete this adaptation. For example, beef bulls reared in the cornbelt in the U. S. until they are two years old and then taken to the harsher range country are mostly too old then to learn how to make a living on the open range. They would have learned that if they had spent their calfhood there. The reproductive cycle may be upset when animals are taken from the Northern to the Southern hemisphere or the reverse. Usually they adjust within a year or so. Similar upsets may occur when they are moved suddenly from a temperate climate to the tropics or from low to extremely high altitudes.

43. These practical and important facts are already moderately well known to stockmen and herdsmen who have made or accompanied importations of animals from one climate to a distinctly different one. This individual adaptation has little or no genetic implication, except insofar as ability to adapt is itself partly conditioned by the animal's genotype.

Fitting the Plans to the Country

44. Animal improvement schemes should be fitted to the present state of husbandry in the area under consideration, or to what seems likely to be the state of husbandry there in the near future. Because improvement by breeding comes slowly, one really should be breeding animals adapted to the conditions which will prevail at least two or three animal generations later, as far as he can estimate now what these conditions will be.

45. Conditions of husbandry may sometimes change rapidly. Resistance to disease and to insect damage may be highly important initially but they will become unimportant if and when cheap and effective methods of disease and insect control are put into use. Perhaps pastures and feed production may be improved so much that in a generation or two different qualities in the animals will be wanted, such as earlier maturity, and less value may be attached to their ability to survive well through periods of submaintenance nutrition. Perhaps such nutritional improvement will not come?

46. Such changes in husbandry or changes in market demand occur, even in the highly developed countries. Robert Bakewell's achievements in animal breeding two centuries ago consisted largely in breeding animals to be fatter at early ages than animals had ever been before. New edible fats of vegetable origin have become far more abundant than in Bakewell's time and pigs and even cattle are being bred with less fat and more lean.

47. Consequently the men who do or guide the animal improvement, need to know the local conditions well. A man from the outside cannot go in and guide the animal improvement schemes effectively. The plans for performance testing and progeny testing need to include provision for training local personnel to operate these plans, and especially to push the extension phases of the plans. These men need access to experiment stations where they can obtain answers to some of the simpler questions

and can measure the individual performance and adaptability of at least those animals in the nucleus breeding herds. First-hand familiarity with the reproductive rates, rearing percentages, and other vital statistics of the species in that region is almost a prerequisite for a man to help wisely in planning animal improvement.

48. Some of the devices for improving animals genetically require keeping individual pedigrees. Sometimes this is not possible. Fencing may be too expensive or other reasons may prevent knowing which male was the sire of each animal. If individual pedigrees are not known, no progeny testing of males is possible and the progeny testing of females is very limited. This will slow down the possible rate of improvement but does not stop it altogether. When the sires are unknown, most of the selection must be done on individual qualities. One can perhaps separate the males and females which seem to be the very best into a top stud flock from which will come the sires to be used in the next generation and keep that stud flock isolated. In this way, even without knowing the individual sires, one can get some (but not all) of the advantages of selection on pedigree.

49. If individual production cannot be measured, the possible rate of animal improvement is much reduced. Then one can only fall back on "eye-ball" judgment, which is reasonably good for some characters but notoriously ineffective for improving others, especially for those aspects of production which are complex and rest more largely on physiological than anatomical differences.

50. The main considerations for long-time progress are assurance of economic stability, reasonable expectation of law and order, and that the owner or local manager of the herd have incentive to use his own initiative and to take some risks. If the local manager is blamed when things turn out wrong but is not given a special reward when they turn out well, he will generally try to take as few risks as possible. If this condition is extreme, he may do little except execute written orders scrupulously, so as not to be blamed. This is more serious in animal breeding than in many other branches of human endeavor, because the actual outcome of animal breeding efforts, especially in herds of small or moderate size, is greatly affected by chance events. Mendelian segregation and recombination keep restoring and introducing individual variability in breeding values. With the finitely small number of sires chosen on any one farm, the man who does the choosing will often be wrong in individual cases, even though he works diligently and intelligently. Knowledge of genetics has reached the stage where one can predict with high accuracy the average result of choosing 1000 sires by method A rather than by method B, but he cannot yet, nor is there any prospect that he ever can predict closely the outcome for each such individual sire. Operationally, animal breeding is much like aiming a shotgun and not at all like aiming a rifle! This may not be entirely a disfavor; any sensible hunter would choose a shotgun for some kinds of game and a rifle for others!

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